MINUARTIA MACRANTHA (ALSINOIDEAE: CARYOPHYLLACEAE): MORPHOLOGICAL CIRCUMSCRIPTION, GEOGRAPHICAL RANGE, AND PHYLOGENETIC AFFINITIES

Ronald L. Hartman

Rocky Mountain Herbarium
Department of Botany
University of Wyoming
Laramie, Wyoming 82071-3165, U.S.A.
rhartman@uwyo.edu

Richard K. Rabeler

University of Michigan Herbarium 3600 Varsity Drive Ann Arbor, Michigan 48108-2228, U.S.A. rabeler@umich.edu

ABSTRACT

Minuartia macrantha is here defined to include M. filiorum. The traditional morphological distinctions between the two reputed taxa are discussed. Previously, M. macrantha was considered endemic to Colorado; now its geographical range is much expanded. Minuartia filiorum (= M. macrantha) is not closely related to M. rubella, contrary to a recent floristic treatment which recognized it as a variety of the latter. Minuartia macrantha is considered a southern counterpart of the M. rossii-stricta complex. This alliance includes the northern Rocky Mountain M. austromontana, recently found sympatric with M. macrantha in northwest Wyoming. Minuartia stricta is discussed briefly as it is often confused with M. macrantha in Colorado.

RESUMEN

Se define aquí *Minuartia macrantha* para que incluya *M. filiorum*. Se discuten las diferencias morfológicas tradicionales entre los dos supuestos taxa. Previamente, *M. macrantha* fue considerada endémica de Colorado; ahora su rango geográfico se ha expandido mucho. *Minuartia filiorum* (= *M. macrantha*) no está cercanamente relacionada con *M. rubella*, contrariamente a un reciente tratamiento florístico que la reconoce como variedad de esta última. *Minuartia macrantha* se considera una equivalente sureña del complejo *M. rossii-stricta*. Esta alianza incluye la norteña de las Montañas Rocosas *M. austromontana*, encontrada recientemente como simpátrica con *M. macrantha* en el noroeste de Wyoming. *Minuartia stricta* se discute brevemente ya que se confunde frecuentemente con *M. macrantha* en Colorado.

Our intent is to elaborate on the morphology of *Micrantha macrantha* s.l. (including *M. filiorum*), and the degree of variability of diagnostic characters. Furthermore, the marked change in geographical range is documented (see specimens cited and Fig. 1). Finally, the presumed phylogenetic affinities of *M. macrantha* are discussed.

Bassett Maguire is recognized for his superb taxonomic treatments of *Arenaria*, including currently recognized segregate genera (*Eremogone*, *Honckenya*, *Minuartia*, and *Moehringia*), in North America and his collaboration with C. L. Hitchcock on *Silene*. Subsequent to Maguire's work, Stanley L. Welsh and associates at Brigham Young University obtained numerous collections from Utah and vicinity that were determined as *M. filiorum*. Correspondingly, floristic studies in Colorado and Wyoming (COLO, RM) contributed a wealth of material, chiefly from these core southern Rocky Mountain states, that were determined as *M. macrantha*. Unfortunately, there was relatively little communication between these two areas, although a number of duplicates were exchanged. When we examined these collections during the preparation of the treatment of *Minuartia* for the *Flora of North America* (Rabeler et al. 2005), we found the specimens filed as *M. macrantha* and *M. filiorum* to be more difficult to segregate than the literature suggested.

MORPHOLOGY

Maguire (1946) described *Minuartia filiorum* and later (1958) distinguished it from *M. macrantha* (both under *Arenaria*) on the basis of habit (annual or weakly perennial vs. obviously perennial with numerous procumbent stems to 10 cm), cymes (1–5- vs. 3(–5)-flowered), flowers (not showy vs. large and showy), sepal length and shape (3.5–4.8 mm, ovate-lanceolate vs. 4.5–5 mm, broadly lanceolate), and petal to sepal ratios (shorter than to equaling sepals vs. conspicuous, exceeding them, to 8 mm long, respectively). While

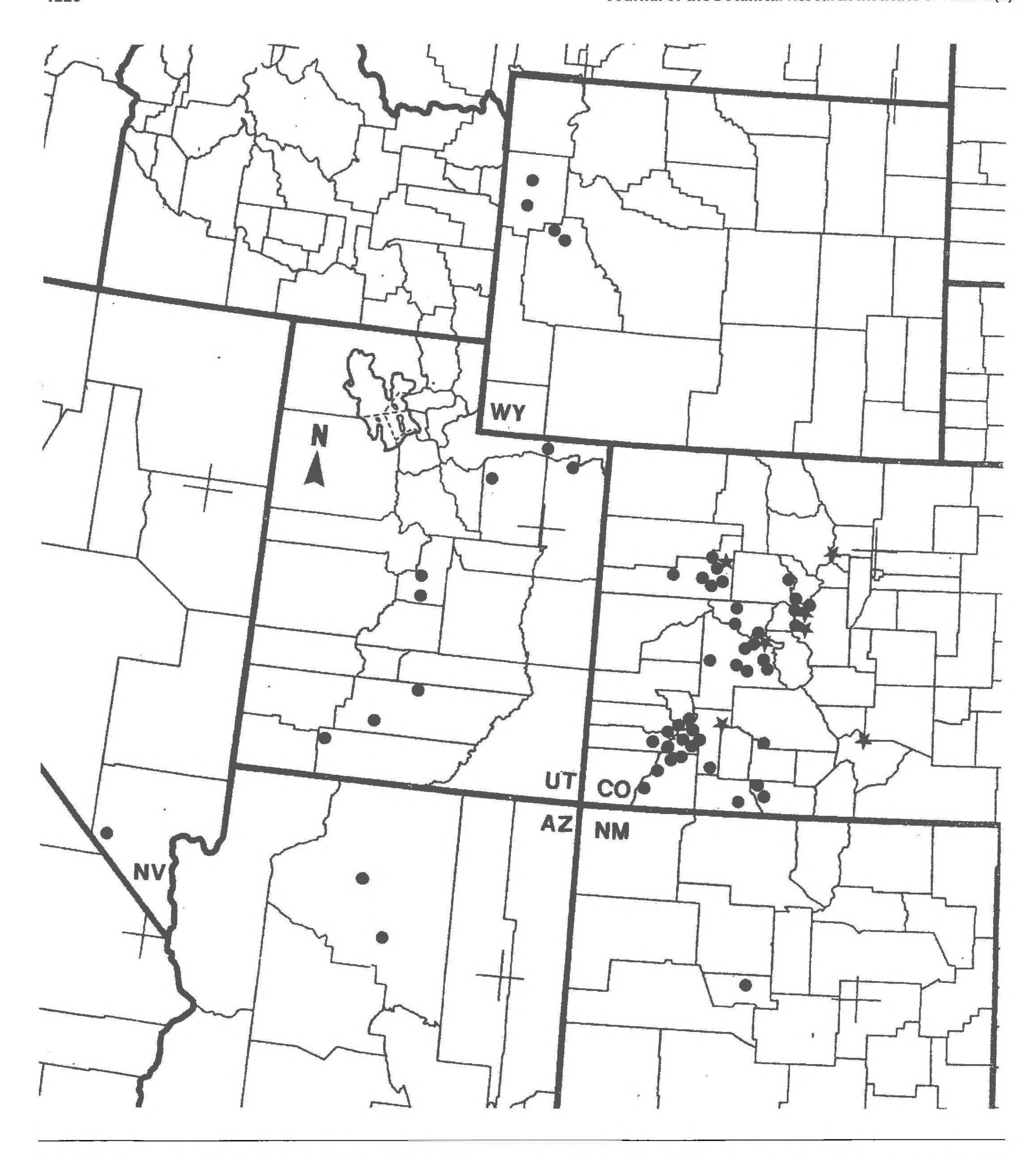


Fig. 1. Map of the southern Rocky Mountains, U.S.A., with solid dots representing collecting sites of *Minuartia macrantha*, solid stars representing sites of *M. stricta*.

some populations may be differentiated using these features, many cannot be so recognized. For example, the number of flowers per inflorescence, the length of the petals relative to the sepals, and sepal length are more variable than portrayed. On the other hand, the mature sepals of both taxa are strongly ribbed (Fig. 2a) and the seeds are essentially identical. We concur with W.A. Weber and R. Wittmann's annotation of the holotype of *M. filiorum* (as *Alsinanthe macrantha* (Rydb.) W.A. Weber 1983) as inseparable from *M. macrantha*; our independent conclusion (Rabeler et al. 2005).

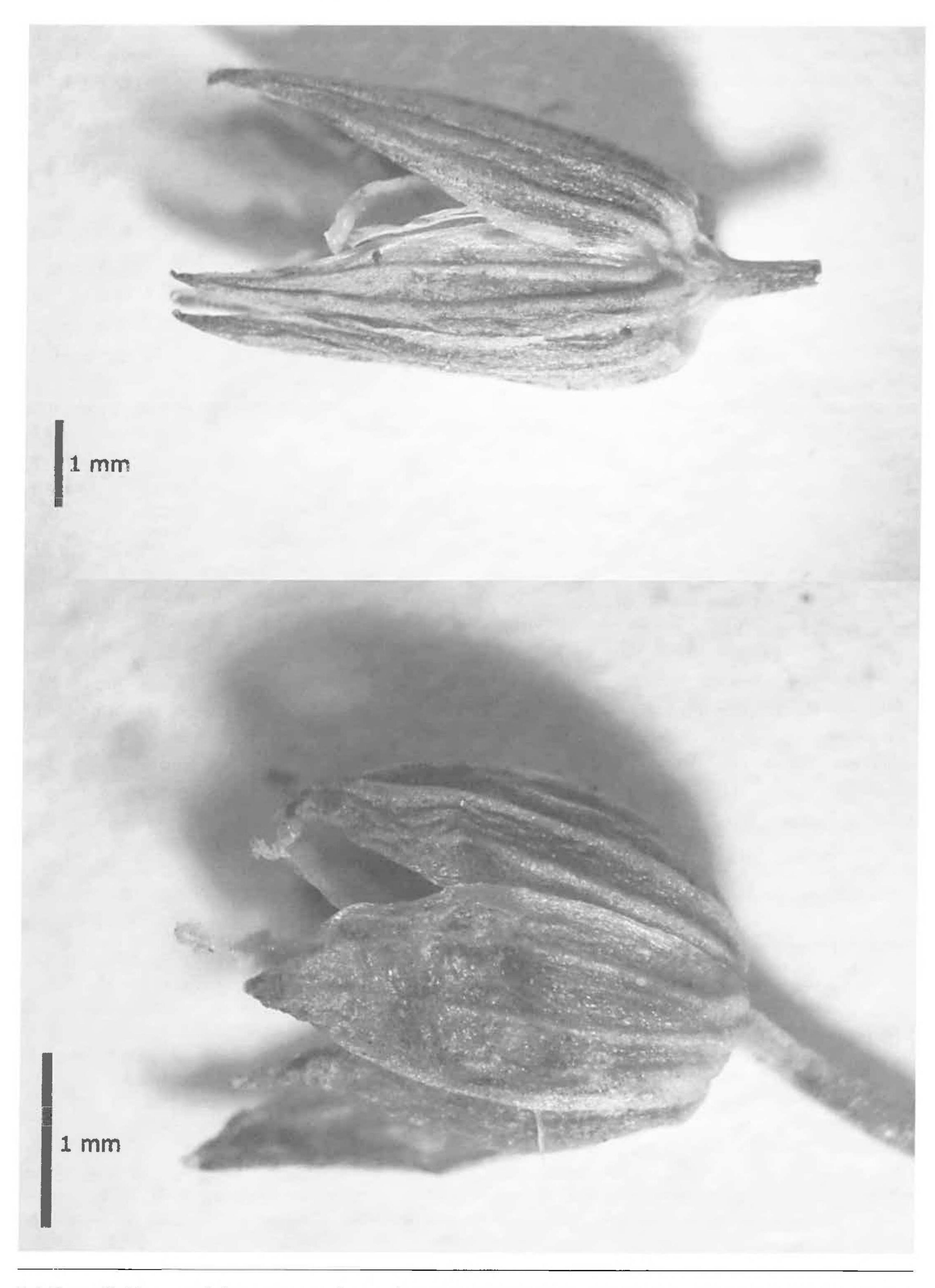


Fig 2. Photos of fruiting material of *Minuartia macrantha* at top (*Huber & Goodrich 2910*, BRY) and *M. stricta* below (*Elliott 11048a*, RM). Note scale bars, the *M. stricta* is magnified 2× relative to *M. macrantha*.

Minuartia macrantha (Rydb.) House, Amer. Midl. Naturalist 7:132. 1921. Alsinopsis macrantha Rydb., Bull. Torrey Bot. Club 31:407. 1904. Arenaria macrantha (Rydb.) A. Nelson, New Man. Bot. Centr. Rocky Mt. 186, 608. 1909, non Schischk. Fl. URSS 6:522, 886. 1936. Alsinanthe macrantha (Rydb.) W.A. Weber, Phytologia 51:369. 1982. Type: U.S.A. Colorado: La Plata Co. [Montezuma Co.]: La Plata Mts., Little Kate Basin, common alpine form, 14 Jul 1898. C.F. Baker, F. S. Earle, & S.M. Tracy 678 (HOLOTYPE: NY, photo!; ISOTYPE: NY, photo!; RM, 2!).

Arenaria filiorum Maguire, Bull. Torrey Bot. Club 73:326. 1946. Minuartia filiorum (Maguire) McNeill, Rhodora 82:498. 1980. Arenaria rubella (Wahlenb.) Sm. var. filiorum (Maguire) S. L. Welsh, Rhodora 95:393. 1993. Type: U.S.A. Utah. Kane Co.: [Iron Co.]: Navajo Lake, [9030 ft], common, gravelly beaches, 13 Jul 1940. B. Maguire 19472 (HOLOTYPE: NY, photo!; ISOTYPE: GH, UTC, UC).

Common nanes.—House's stitchwort, large-flower sandwort, beach sandwort.

Plants perennial, cespitose or mat-forming, or sometimes annual, glabrous throughout. Taproots occasionally filiform, but usually somewhat thickened to moderately stout, often woody. Stems erect to numerous and procumbent, green, 2-20 cm long, internodes of all stems 0.3-1(-2) times leaf length. **Leaves** moderately to tightly overlapping (proximal cauline), variably spaced, progressively more so distally (distal cauline), connate proximally, with loose, scarious sheath 0.3-0.8 mm long; blade straight to slightly outcurved, green, flat to triquetrous distally, 1–3-veined, fleshy, midvein more prominent than 2 lateral veins, subulate to linear, 5–10 mm long, 0.5–1.2 mm wide, flexuous, margins not thickened, scarious, smooth, apex green, rounded, thickened and navicular, shiny; axillary leaves present among proximal cauline leaves. Inflorescences terminal, 2–5(–9)-flowered, open to strict cymes or more often a solitary flower; bracts broadly subulate, herbaceous or scarious-margined proximally. Pedicels 0.2-1.5 cm long. Flowers perigynous, 5-merous; hypanthium disc-shaped; sepals ovate to lanceolate (herbaceous portion lanceolate), 3.5–5.5 mm long, to 6.5 mm in fruit, margins thinly scarious (0.1–0.2 mm wide), inrolled near apex, strongly 3-ribbed, especially in fruit, rarely weakly so, ribs rounded, apex green or purple in part, blunt to sharply acute or acuminate, not hooded but often incurved; petals oblong to obovate, (0.7–)1.2–1.5(-2) times sepal length, apex rounded to blunt, entire (Fig. 2); stamens 10, those opposite the sepals with basal nectaries 0.3-0.4 mm long, 0.4-0.5 mm wide, triangular, tapering distally, each with a shallow adaxial groove, collectively with the brief hypanthium forming a nectar dish; styles 3, filiform, 1–3 mm long with stigmatic papillae capitate or nearly so. Capsules on stipe ca. 0.2 mm long, broadly ovoid, 3–3.8 mm long, somewhat shorter than to slightly exceeding the sepals, valves 3, recurved at apex. Seeds 8–13, black, suborbiculate with radicle prolonged to rounded beak, somewhat compressed, 0.7–1 mm long, tuberculate; tubercles low, rounded.

Representative specimens: Collections either cited or annotated as *Arenaria filiorum* by Maguire are indicated by an "**m**" followed by the herbarium abbreviation and literature citation where appropriate (e.g., (**m**; USFS), (**m**; NY, UTC, cited Madroño 8:262. 1946)). Up to three collections are cited per county.

UNITED STATES. ARIZONA. Coconino Co.: San Francisco Mts., 12,000 ft, 7 Aug 1938, Little 4664A (USFS); Kaibab Plateau, De Motte Park, 8,700 ft, 17 Jun 1977, Reeves 5634 (ASU). COLORADO. Archuleta Co.: Quartz Lake trail, 6 Sep 1998, Heil 12 (SJC). Clear Creek Co.: Grays Peak, Jul 1888, Eastwood s.n. (COLO). Conejos Co.: S of Blue Lake, 12,000 ft, 17 Jul 2003 Lundquist & Rink L118 (RM). Dolores Co.: Navajo Basin, 11,140-12,100 ft, 26 Jul 1994, Moore 3441 (RM); upper Fish Creek drainage S of Dolores Peak, 10,200-11,800 ft, 27 Jul 1995, Moore 7533 (RM). Garfield Co.: head of East Elk Creek, Flat Tops, 10,000-10,400 ft, 24 Jul 1990, Hartman 25915 (RM); Clinetop Mesa, 10,300-10,500 ft, 24 Jun 1990, Hartman 25938 (RM); Indian Camp Pass, 9,800-10,000 ft, 6 Aug 1991, Vanderhorst 3824 (RM). Gunnison Co.: Horse Basin, 11,600 ft, 7 Aug 1950, Langenheim 70 (COLO); Comanche Creek, 12,000 ft, 14 Jul 1951, Langenheim 1361 (COLO); Fossil Ridge area, 12,450 ft, 30 Jul 1989, Lehr 1262 (COLO); Double Top Mt., 11,500-11,900 ft, 14 Jul 1997, Taylor 3293 (RM). Hinsdale Co.: Graham Peak area, 10,420-11,425 ft, 11 Jul 2002, Heil & Mietty 19182 (SJC). Lake Co.: Weston Pass, 12,000 ft, 14 Jul 1940, Gierisch 1298 (USFS). La Plata Co.: Silver Mesa near Lake Marie, 12,200 ft, 11 Jul 1993, Cramer 67 (COLO); Chicago Basin, 12,000 ft, 13 July 1934, Penland 1075 (COLO); Lime Mesa, 21 Aug 1982, Siplivinsky & Beck 4897 (COLO). Park Co: Weston Pass, 11,700 ft, 28 Jul 1985, Hartman 6357 (RM); Mt. Bross, 3,500-3,900 m, 25 Jul 1982, Weber et al. 2115 (COLO, RM); North Star Mt., 12,300 ft, 3 Jul 1954, Weber 8751 (COLO). Pitkin Co.: ridge E of Avalanche Ck, 12,000 ft, 14 Jul 1952, Langenheim 2106 (COLO). Rio Grande Co.: Wet Canyon, 2.6 mi NW of Elwood Pass, 10,500 ft, 24 Jul 1996, Heil 10367 (SJC). San Juan Co.: near Ironton, 21-31 July 1899 Curtis s.n. (m; NY); Ruby Pass, 12,700 ft, 6 Jul 1996, Hogan 3023b (COLO); Stony Basin, 12,500 ft, 29 Jul 1983, Rottman 1753 (COLO). San Miguel Co.: near Trout Lake, 12,000 ft, 21 Aug 1924, Payson & Payson 4192 (RM). NEVADA. Clark Co.: Charleston Peak, 3,400 m, 8 Aug 1935, Clokey 5460 (m; NY, UTC). NEW MEXICO. Bernalillo Co.: Kiwanis Point, Sandia Crest, 15 mi NE of Albuquerque, 10,000-10,200 ft, 28 Jul 1964, Baad 1035 (MICH), 23 Jun 1976, Wagner 2344 (MO), 22 Jul 1999, Sivinski 4997 (RM, UNM) (see Hartman and Sivinski 2006). UTAH. Beaver Co.: Tushar Mts., Dugway above Big Jim Flat, 3,050-3,150 m, 27 Jul 1991, Atwood 16176 (BRY). Daggett Co.: "Gates of Birch Creek," 8 mi WSW of McKinnon, Wyoming, 9,600-9,700 ft, 30 Aug 1984, Tuhy 2176 (UTC). Duchesne Co.: S rim of S

Fork Rock Creek, 14 mi N of Tabonia, 10,700 ft, 29 Jul 1981, Goodrich & Jepson 15904 (BRY, RM); S rim of S Fork Rock Creek, T2N R8W Sec. 24, 10,700 ft, 15 Aug 1995, Huber & Goodrich 2910 (BRY); Boulder Mt., 9,800 ft, 17 Aug 1995, Welsh & Atwood 26242 (BRY, COLO). Garfield Co.: T31S R3E Sec. 36, 10 Sep 1942, Ellison 942-13 (USFS); Clinetop Mesa, 10,300–10,500 ft, 24 Jun 1990, Hartman 25938 (RM); Boulder Mt., Pleasant Creek Meadows, 10,600–10,700 ft, 6 Aug 1996, Huber 3415 (BRY); 2 mi N of Posey Lake, Aquarius Plateau, 10,000 ft, 29 Jun 1940, Maguire 20105 (m; NY, cited Madroño 8:262. 1946). Iron Co.: ¼ mi E Brian Head Peak, 11,000 ft, 23 Jun 1940, Maguire 20097 (m; NY, UTC); summit of Second Left Hand Canyon, Markagunt Plateau, 3,100 m, 9 Aug 1986, Neese 17615 (m; BRY). Juab Co.: Mt. Nebo, 10,500–11,500 ft, 17 Jul 1980, Collins & Harper 864 (BRY). Kane Co.: Spruce Camp, Navajo Lake, 15 Jul 1940, Maguire 19541 (UTC). San Pete Co.: head of Mayfield Canyon, 10,928 ft, 8 Aug 1940, Maguire 19988 (m; NY, UTC, cited Madroño 8:262. 1946); T20S R4E Sec. 19, 10,000 ft, 22 Aug 1945, Ellison 4533 (m; USFS); Heliotrope Mt., 11,000 ft, 24 Jun 1977, Lewis 4760 (BRY). Uinta Co.: Dyer Mine, 5 Jul 1902, Goodding 1256 (RM). WYOMING. Sublette Co.: Palmer Peak, 10,600–11,400 ft, 5 Aug 1994, Hartman 40378 (RM); Hodges Peak, 10,400–11,180 ft, 2 Aug 1994, Hartman 49240 (RM). Teton Co.: Moose Basin divide, 9,140 ft, 22 Aug 2007, Scott & Varga 5711a (RM); Mount Hunt divide, 9,700 ft, 4 Aug 2004, Varga et al. s.n. (Grand Teton National Park).

GEOGRAPHIC RANGE, ECOLOGY, AND PHENOLOGY

Prior to Rabeler et al. (2005) and Hartman and Sivinski (2006), the published geographical range of *M. macrantha* s.str. was Colorado while *M. filiorium* was credited to the southern portions of Colorado, Utah, and Nevada (Maguire 1946, 1958). Based on recent collections and annotations, *M. macrantha* s.l. is now known to occur throughout western Colorado, from northeast to southwest Utah, at one location in southern Nevada, and most recently in restricted areas of central Arizona, central New Mexico, and northwest Wyoming (see specimen citations and Fig. 1).

Minuartia macrantha is commonly found on limestone substrates although a few labels indicate volcanics. Habitats vary from Festuca idahoensis Elmer meadows to parklands and other open areas often associated with Picea engelmannii Parry ex Engelm., Abies bifolia A. Murray bis, Pseudotsuga menziesii (Mirb.) Franco, Populus tremuloides Michx., and Pinus contorta Douglas ex Loudon var. latifolia Engelm. With increase in elevation, it is found in krummholtz and alpine meadows, ridges, and scree and talus slopes. The elevational range is 2100–3700 m.

Flowering extends from early June into September; mature fruits are not seen until late July to September.

PHYLOGENETIC HYPOTHESES

The relationships between Minuartia (Arenaria) macrantha s.str., M. filiorum, M. rubella, and the M. rossii-stricta complex (Wolf et al. 1979; McNeill 1962) have been in dispute.

Relationship of Minuartia macrantha to Minuartia rubella (sect. Tryphane)

In preparation for the flora of Utah, Welsh (1993) transferred *Arenaria filiorum* to a variety of *A. rubella*. He distinguished var. *filiorum* from var. *rubella* by herbage (glabrous vs. typically glandular), sepal length (3.5–6.7 mm. vs. 2.8–4.5 mm), and seed length (0.7–1 mm. vs. 0.4–0.6 mm, respectively). Comparable character states (Welsh et al. 2003) for *A. macrantha* are: herbage glabrous, sepals 4–5 mm long, seeds 0.7–1 mm long.

Under *M. macrantha*, Welsh et al. (1993) provided the following comment: "The plant, long obscured within the mass of *A. rubella* in Utah collections, is still poorly known, and might represent nothing more than an extreme phase of that species. It stands mainly on the feature of petals substantially surpassing the sepals, which are longer than for *A. rubella* var. *rubella*, but not for *A. rubella* var. *filiorum*."

In contrast to Welsh's quotes, *Minuartia macrantha* s.l. and *M. rubella* are quite distinct; the two species are easily distinguished in the field without magnification. The former is consistently glabrous while *M. rubella* is invariably and prominently stipitate-glandular throughout the vegetative structure (see Rabeler et al. 2005). Furthermore, the two species differ in leaf morphology (1-nerved, fleshy vs. 3-nerved, not fleshy) and seed size (0.7–1 mm vs. 0.4–0.7 mm, respectively).

The relationship between *M. macrantha* s.l. and *M. rubella*, is distant at best (see below). *Minuartia macrantha* is restricted to the western United States while the latter taxon is circumboreal extending south into western North America. Maguire (1958) considered *Arenaria macrantha* s.str. and *A. filiorum* to be "the southern complement of *A. rossii*" and did not include *Minuartia* (*Arenaria*) rubella in this complex. In fact,

M. rubella traditionally has been placed in the highly polymorphic Minuartia section Tryphane (Fenzl) Hayek (3–10 taxa), and is the sole member found in North America (McNeill 1962). The lectotype for the section Tryphane is M. verna (L.) Hiern (chromosomal base x = 12, see below), with which Minuartia rubella has often been confused.

Relationship of Minuartia macrantha with sects. Sclerophylla versus Alsinanthe

Two other relevant sections of Minuartia recognized by McNeill are Sclerophylla Mattf. (lectotype, M. michauxii (Fenzl) Mattf.) and Alsinanthe (Fenzl) Graebn. (lectotype, M. stricta (Sw.) Hiern). Section Sclerophylla is quite heterogenous and consists of seven species. Two of these taxa were not seen (=?) by McNeill: ?Arenaria filiorum and ?A. macrantha. Consequently, he did not make the combination Minuartia filiorum at that time. In our opinion, neither of these taxa belong in this section, one characterized in part by "leaves rigid, recurved and very thick median nerve."

Weber and Wittmann (2000) recognize *Tryphane rubella* (Wahlenb.) Rchb. on one hand and *Alsinanthe macrantha* and *A. stricta* (Sw.) Rchb. on the other. This generic realignment was predicated in part on different chromosomal base numbers: x = 12 for *Tryphane* (Hartman 1971; Löve and Löve 1975a and x = 15 for *Alsinanthe* (Löve & Löve 1975a). Although there are no known chromosome counts of *M. macrantha*, one with a base number of x = 15 would be consistent with Maguire's notion of *M. macrantha* being closely related to *M. rossii*. Wolf et al. (1979) reported counts based on x = 15 for the three members of the *M. rossii* complex, a base number also documented for *M. stricta* (Löve & Löve 1975b). Recent molecular investigations of the Caryophyllaceae have included *Minuartia* (Nepokroeff et al. 2001, Fior et al. 2006) and both suggested that *Minuartia* is polyphyletic. Nepokroeff et al. (2001 and pers. comm.) found *M. rubella* and *M. rossii* appearing in unrelated clades; unfortunately, *M. macrantha* was not sequenced.

Distribution of the Minuartia macrantha

Previously, comments were made as to a possible affinity of Minuartia macrantha s.l. to the M. rossii complex. Wolf et al. (1979) recognized three species in this alliance: M. rossii, M. elegans (Cham. and Schltdl.) Schischk., and M. austromontana Wolf and Packer. The last was a substitute name for Arenaria rossii var. apetala (Maguire non Fenzl; see Hartman and Nelson 1998, p. 57). The first two species are largely high Arctic in distribution whereas M. austromontana extends south along the spine of the Rocky Mountains from central Alberta, Canada, through Montana and west-central Wyoming, with a disjunct population in the Wallowa Mountains, Oregon, U.S.A. (Cusick 2299, in part, GH!; Peck 22576, WILLU! at OSC). One geographic outlier from the Uinta Mountains, Utah (Harrison & Harrison 10926, BRY!) cited by Wolf et al. (1979) represents a specimen of M. macrantha. In Wyoming, four historical records (pre-1960, RM, USFS; Wolf et al. 1979) of M. austromontana were known from the Beartooth Plateau, the Teton Range, and the northern Wind River Range. Based on recent collections (1978–2007, RM), 41 additional sites have been documented from the Absaroka, Gros Ventre, and Teton Ranges and the Big Horn Mountains. By contrast, the southern Rocky Mountain M. macrantha is now documented from Wyoming; an apparent disjunct from the northeastern Utah or northern Colorado. It is known from three sites (1994–2007, RM) from the Teton Range and the Gros Ventre Mountains. Other state records include Arizona and New Mexico.

Both *M. austromontana* and *M. macrantha* are sympatric in the Gros Ventre Range of northwestern Wyoming with no hint of hybridization. Their differences in gestalts and detailed morphology allow for easy separation (see Rabeler et al. 2005; *M. rossii*, *M. elegans*, *M. austromontana*, and *M. macrantha* appear near one another in the key to species of *Minuartia*, couplets 37 to 42).

Distribution of Minuartia stricta relative to Minuartia macrantha in Colorado

Minuartia stricta (Sw.) Hiern also occurs in Colorado and is disjunct in California as well from its normal range that extends from Alaska, across northern Canada, to Greenland and Eurasia (Rabeler et al. 2005, Nannfeldt 1954). It is here mentioned as it is frequently confused with *M. macrantha*. The key to species of *Minuartia* (Rabeler et al. 2005) is terminated by *M. stricta* and *M. dawsonensis* (Britton) House (couplet 43). *Minuartia macrantha* and *M. stricta* differ as follows: sepals 3.5–5 mm vs. (1.5–)2.5–3.2 mm long in flower,

to 5.5 mm vs. 4 mm long in fruit (Fig. 2); seeds 0.4–0.6 mm vs. 0.7–1 mm long, respectively; and subtle leaf and habit differences. The documented distributions of *M. macrantha* and *M. stricta* in Colorado, where they are known to co-occur, are shown on Fig. 1.

Specimens of *Minuartia stricta* in the southern Rocky Mountains are listed below (based on holdings at COLO and RM):

COLORADO. Boulder Co.: above Needles Eye tunnel at Rollins Pass, 11,300 ft, 18 Jul 1969, Brown 38 (COLO). Garfield Co.: E side of Heart Lake, 10,600 ft, 26 Jun 1963, Miller 300 (COLO). Gunnison Co.: North Italian Mountain, 13,300 ft, 1 Aug 1949. Langenheim 455 (COLO). Hinsdale Co.: Mesa Seco, above Spring Pass, 12,400 ft, 31 Jul 1964, Weber 12167 (COLO). Huerfano Co.: 0.5 mi W of Iron Nipple, 12,000 ft, 17 Aug 1999, Elliott 11048a (RM). Park Co.: Sheridan Mountain, above Hilltop Mine, 13,790 ft, 12 Jul 1967, Weber 13303 (COLO); Hoosier Ridge, east of pass, 12,500 ft, 8 Jul 1951, Weber et al. 6551 (COLO). Summit Co.: Hoosier Ridge, 12,000 ft, 10 Jul 1959, Hultén & Weber 11054a (COLO).

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